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original article

Untangling the reticulate history of species complexes and horticultural breeds in *Abelia* (Caprifoliaceae)

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ABSTRACT

• **Background and Aims** The genetic and morphological consequences of natural selection and selective breeding are explored in the genus *Abelia*. The genus consists of ornamental shrubs endemic to China, which have been bred to create attractive and diverse cultivars.

• **Methods** We use DNA fingerprinting (AFLP) and DNA sequence data to investigate the genetic diversity among 46 accessions of *Abelia* (22 natural taxa and 24 horticultural breeds). In the cultivated varieties these data are used to explore taxon boundaries, hybridisation and backcrossing. The dataset is also used to investigate morphological variation within natural species complexes and subsequently to inform a taxonomic treatment.

• **Key Results** *Abelia* comprises five species: *A. forrestii*, *A. schumannii*, *A. macrotera*, *A. uniflora* and *A. chinensis* and has a total of 11 varieties. *Abelia uniflora* and *A. macrotera* do not occur in sympatry and are disjunctly distributed to the east and west of the *A. chinensis* distribution range. *Abelia chinensis* is widespread in eastern China and creates hybrids and introgressive taxa, including *A. uniflora*, along the contact zones with the previous taxa. *Abelia* 'Maurice Foster' is a horticultural variety collected from wild stocks in Sichuan (China). Bayesian clustering methods (inferred in STRUCTURE based on AFLP data) indicate admixture between *A. macrotera* and *A. schumannii* in this variety. We can infer that hybridization probably occurred in the wild where these progenitor taxa co-occur and naturally form hybrids. AFLP results also reveal that a few diagnostic morphological characters such as sepal number or inflorescence structure were transferred between natural species are mirrored by horticultural crosses such as in *Abelia* 'Saxon Gold' and *A. forrestii*.

• **Conclusions** Studying both natural and cultivated species from the same group has enabled us to understand both differentiation mechanisms and how to improve cultivated plants in the future by studying which morphological characters are transferred between species and which taxa may already have arisen through hybridisation.

Keywords: *Abelia*; AFLP; hybridization and introgression; cultivars; nomenclature; China.

Short Title: *Abelia* hybridization and introgression

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INTRODUCTION

Described by Robert Brown in 1818 (Brown, 1818) the genus *Abelia* is known for its widely cultivated hybrid, *A.* x *grandiflora*, commonly cultivated as a trimmed hedge around the world. Although its breeding history is documented, exactly how it relates to the wild taxa occurring in China remains unclear. The hybrid is said to have been obtained in Italy by MM. Rovelli Brothers Nurseries in Pallanza (Lake Maggiore), a cross between *Abelia chinensis* and *A. uniflora* (André, 1886). *Abelia* is a genus endemic to China with between three and 15 taxa, depending upon which circumscription is followed. It is regarded as a species complex with difficult taxonomic treatment. Most specimens of *Abelia* examined are diploid (Kim, 1998) and probably self-incompatible (Scobie and Wilcock, 2009), they do not vegetatively reproduce but are propagated clonally by cuttings in cultivation. Viable seed production is low and achenes are wind dispersed, though dispersal distances have not been studied.
The current study aims to compare and contrast the genetic signature of selective breeding and genetic differentiation in the genus *Abelia*. To improve the feasibility of this study we first needed to have a clear idea of the morphological variation, distribution and nomenclature of the naturally occurring taxa of *Abelia* in China as well as those in cultivation. We have devised a new nomenclature and studied in detail the morphological and genetic variation within *Abelia* and how selective breeding and hybridisation could give answers to the species concept.

Mechanisms of differentiation

Polyploidization and hybridization are among the most important forces in the evolution of higher plants and at least 25% of the plant species are involved in hybridisation and introgression with other species (Mallet, 2005, 2007). Hybrids combine different genotypes and generate phenotypic traits that are often intermediate between their parents and that in turn is often used as evidence for hybridization in morphological analyses. If backcrossing with one or both the parental taxa occurs repeatedly, i.e. introgression occurs, the parental taxa successively incorporate parts of the genome from the other taxa involved in hybridization and further increase the number of morphological transitions between the species as demonstrated in other studies (Rieseberg, 1997; Hardig *et al*., 2000). Uncovering hybridization and introgression is important to reveal the origin of species and to obtain insights into the processes behind the intra- and interspecific variability.

Interspecies hybridization is a method that is often used in horticultural breeding programmes, wild relatives are used as donors of desirable traits for the cultivated plants (for example disease resistance). Provenance and sometimes identity of the parents are rarely documented, this problem is more acute in groups of species or species complexes where taxa are morphologically similar and difficult to distinguish: 'Some of the confusion in the naming of cultivated material appears to derive from a failure to recognise the great variability of some wild taxa' (Barnes, 2001). Breeding programmes are nevertheless a model to study hybridisation and its consequences because artificial hybrids unlike wild populations are not involved in uncontrolled introgression or selection which would blur limits between taxa. Cultivars and hybrids could therefore be a model to trace back the crossing history of wild taxa and the consequences on their phenotypic traits. Incomplete lineage sorting is nevertheless also to be taken into account.

One approach for identifying hybrids uses incongruences between phylogenies based on maternally (cpDNA) and nuclear genes inherited markers (Cronn *et al*., 2003; Clarkson *et al*., 2010). A premise is that the phylogenetic resolution of the studied markers is sufficient to distinguish taxa suspected to be involved in hybrid formation. This is often not met in plastid DNA regions which generally have low substitution rates (Wolfe *et al*., 1987). In recent years, a number of molecular markers, e.g., random amplified polymorphic DNA (RAPD;

(Williams *et al*., 1990)), amplified fragment length polymorphism (AFLP; (Vos *et al*., 1995)) simple sequence repeats (SSR; (Zietkiewicz *et al*., 1994)) and inter-simple sequence repeats (ISSR) have been widely used to detect genetic diversity in plants (Nybon and Bartish, 2000). Various other ornamental plants have been used for DNA marker based diversity studies using AFLP including *Nelumbo* (Hu *et al*., 2012), *Rosa* (Koopman *et al*., 2008), yellow Camellia (Tang *et al*., 2006). AFLP was used in studies of two related *Abelia* genera, *Diabelia* in Zhejiang (Zhou *et al*., 2004) and *Dipelta* in Gansu (Liu *et al*., 2013).

MATERIALS AND METHODS

Sampling

A total of 55 samples were collected mostly from the trial field experiment at RHS Wisley (UK) spanning the morphological and geographical variability within targeted taxa (Appendix 1).

DNA extraction

Genomic DNA was extracted using a modified cetyltrimethylammonium bromide (CTAB) method (Doyle and Doyle, 1987) using 0.2 g of silica dried leaf tissue. A standard protocol was used to obtain purified DNA (Mikulášková *et al*., 2012).

ITS and cpDNA sequences

Published and unpublished sequences were gathered from two previous studies by Landrein *et al.* (2012) and Hua Feng *et al.* (2014). See publications for detailed methods and Table 1 for gene Bank numbers. *Vesalea floribunda* was selected as an outgroup based on previous data. Phylogenetic analyses were performed using PAUP* v4b10 (Swofford, 2002) for maximum parsimony (MP) analyses, and MrBayes 3.2.2 (Ronquist and Huelsenbeck,

2003) for Bayesian inference (BI). The MP analyses used heuristic searches with 1,000 random addition sequence replicates, tree bisection reconnection (TBR) branch swapping, and MULTREES on. All character states were treated as unordered and equally weighted with gaps treated as missing data. To evaluate the relative robustness of clades in the MP trees, a bootstrap analysis (Felsenstein, 1985) was performed with 1,000 replicates using the same options as above except that a maximum of 100 trees were saved per replicate. MrModeltest 2.3 (Nylander, 2004) was run for each of the data sets to determine the most appropriate substitution models using the Akaike criterion (Posada and Buckley, 2004) (see the final row of Table 1). To estimate support for each node, 1 000 bootstrap replicates were performed with automatic termination at 10,000 generations, All final runs were performed on the CIPRS Science Gateway (http://www.phylo.org/portal2/) (Miller *et al.*, 2010). A partitioned Bayesian analysis of the plastid dataset was also implemented by applying the previously determined models to each data partition (Brown and Lemmon, 2007). ITS was found to be incongruent with the plastid analysis and the two were not combined as shown in Landrein *et al.* (2012) and Wang *et al.* (2015). For BI 40 million generations were run with four chains, each starting with a random tree. Trees were sampled every 1,000 generations. Posterior probabilities (PP) were calculated from the majority consensus of all the sampled trees. When the standard deviation of the split frequencies (SDSF) permanently fell below 0.01, 10% of the trees sampled during the burn-in phase were discarded. All final runs were performed on the CIPRS Science Gateway (http://www.phylo.org/portal2/) (Miller *et al.*, 2010).

AFLP amplification and scoring

Reactions were performed following the protocol of Arrigo *et al.* (2010). After performing a primer trial with 24 primers, three selective primer pairs were chosen (*Eco*R1-

ACG/*Mse*1-CTA; *Eco*R1-AAG/*Mse*1-CAC and *Eco*R1-ACC/*Mse*1-CTG), with JOE and NED-labelled *Eco*R1 primers. PCR products were mixed with a Rox size standard ladder and analysed with an ABI 3730XL capillary sequencer. In order to detect and calculate the size of AFLP bands, raw electropherograms were analysed using Peakscanner (ABI) with default parameters except a light peak smoothing. A binary matrix of AFLP band presence (1) and absence (0) was built using the automated scoring RawGeno package (R CRAN; (Arrigo *et al.*, 2009)) with the following parameters: scoring range, 50-400 bp; minimum intensity, 100 rfu; minimum bin width, 1 bp; maximum bin width, 1.5 bp. Closely sized bins were eliminated.

Individuals were randomly distributed in 96-well plates in order to produce a reliable AFLP dataset. 53 samples (representing 22% of the final dataset) were randomly chosen from each plate and replicated to calculate the error rate (Bonin *et al.*, 2004). Bands that were clearly not reproducible were discarded from further analysis. Population structure was analysed with STRUCTURE v.2.3.2.1 (Pritchard *et al.*, 2000) using an admixture model. Bayesian estimates of genetic clustering probabilistically assigns individuals to populations defined by allele frequencies at multiple loci. (Pritchard & al 2000). Parameters selected were: 5000 burn-in repetitions and 50000 MCMC simulations at four iterations.

Our *Abelia uniflora* extraction was unsuccessful with AFLP protocols, as this requires higher molecular weight DNA but this species was included in the DNA sequencing analyses.

To assess the best *K* for the results from STRUCTURE were analysed in CLUMPAK (a program for identifying clustering modes and packaging population structure inferences across K by Kopelman, Naama M; Mayzel, Jonathan; Jakobsson, Mattias; Rosenberg, Noah A; Mayrose) according to the Evanno method (Evanno *et al.*, 2005).

RESULTS

CpDNA-based phylogeny

For 24 taxa, the number of characters was 2232, 321 (14.4%) of which were variable and 168 (7.5%) of which were potentially parsimony informative. The number of characters contributed by each individual region was 604 from *rbcL*, 849 from *trnL-F* and 779 from *matK*. Details for each region are provided in Table 1.

Abelia x grandiflora and *Abelia chinensis* form a clade (BP 54/ PP 0.96, Fig. 1) and a polytomy with *A. macrotera* var. *deutziaefolia*. Both varieties of *Abelia forrestii* form a clade (BP 99, PP 1, Fig. 1) but there is no resolution for the rest of the taxa. *A. x grandiflora* from Zhejiang is sister to *Abelia x grandiflora* originating in Europe (BP 78/ PP 1 Fig. 1).

ITS

For 18 taxa, the number of characters was 637, 65 (10.2%) of which were variable and 40 (6.2%) of which were potentially parsimony informative. Details are provided in Table 2. The monophyly of the genus *Abelia* is weakly supported (PP 0.57, Fig. 2) and *Abelia uniflora* forms a clade with *A*. x *grandiflora* (BP 91/ PP 1, Fig. 2). *Abelia schumannii* and *A. macrotera* form a separate clade (BP 78/ PP 1).

AFLP

Replicate samples indicated high reproducibility of the AFLP data, with the error rate being 0.0%. Altogether, 488 AFLP markers were scored; 300 (61%) of these markers were polymorphic. Details for each region are provided in Table 2.

A Neighbour Joining Tree (Fig. 3) and PCoA (Fig. 4) revealed four clusters that correspond to individuals of

1. *Abelia chinensis* and backcrosses
2. *Abelia macrotera*
3. *Abelia schumannii*, *A. macrotera* x *schumannii* 'Maurice Foster', *A.* 'Saxon Gold' and *A.* 'Edward Goucher'
4. *Abelia* x *grandiflora* and *A. forrestii*

Abelia forrestii is sister to *A. macrotera* and *A. schumannii* but clusters with *A. x grandiflora* in the PCoA.

Within *A. x grandiflora* genetic variability was low and three groups can be identified:

1. *Abelia* x *grandiflora* 'Sherwood'
2. *Abelia* x *grandiflora* 'Francis Mason'
3. *Abelia* x *grandiflora* 'Little Richard'

Dwarf, variegated plants can be found in all three groups. 'Sherwood'-like flowers with basal spurs and dark leathery leaves can also be found in two groups 'Sherwood' and 'Little Richard'.

The results generated by STRUCTURE give some indication on the origin of *A.* x *grandiflora* and admixture of alleles. The analysis provided strongest support for $K = 2$ when considering ΔK and $K = 4$ when considering LnP(Pr data). We identified a substructure at K=5 in which populations appeared homogeneous in their admixture composition. Higher values of K yielded noise that appeared as ancestry shared by very few individuals within the same populations. Cultivated taxa with fully traceable breeding histories such as *A.* 'Edward Goucher' (*A.* x *grandiflora* x *schumannii*) were also used to verify the best *K*.

The five populations identified are (Fig. 5):

1. *Abelia macrotera*
2. *Abelia schumannii*
3. *Abelia forrestii*

4. *Abelia chinensis*
5. *Abelia x grandiflora*

Admixture was identified in *A. macrotera* x *schumannii* 'Maurice Foster', wild collected in Sichuan, at a contact zone between the two taxa. Admixture is also shown with *A.* 'Edward Goucher' as known from the breeding records, as well as in *A.* 'Saxon Gold' with *A. schumannii,* which had not been recorded previously. Backcrosses with *A. chinensis* ('Canyon Creek'; 'Pleasant surprise'; 'Rose Creek') also show admixture with *A. chinensis* as informed by the breeding records and the results shown here. No admixture was identified for *A. x grandiflora* suggesting one of the parents was not present in the sampling or the parents are themselves also the result of hybridisation and introgression in the past (Baack and Rieseberg, 2007).

Abelia morphological study and nomenclature

The AFLP analysis (detailed previously) identified 5 natural taxa in *Abelia.* However, these taxa do not correspond with the current taxonomy and therefore there is a need to re-examine morphological characters and make some refinements to the classification for the group. The current taxonomy for the genus was last revised by Rehder (Rehder 1911) and was useful in assessing the morphological diversity within the group. Some characters can be misleading especially in many cryptic taxa which are sometimes morphologically distinct, but are difficult to assess because their genetic histories are unknown.

Here are presented the results of an analysis of herbarium specimens from 16 herbaria (A, BM, CAS, CDBI, E, GXMI, HENU, HIB, IBK, IBSC, K, KUN, LBG, P, PE, W: acronyms according to Holmgren *et al.* (1990)), published literature sources, including all of the Chinese regional Floras and field observations. A full revision of the genus will be published separately (Landrein in prep).

Abelia was first monographed by Graebner (1901), 10 species were recognised, three more species were added by Rehder (1911) and this was reduced to only five species in *Flora Sinica* (Hsu *et al*., 1988). A total of 25 names have been published.

In this study we recognise five species and 11 varieties. Morphological variation between specimens (761 specimens studied) could mostly be attributed between only two character states such as bilabiate versus infundibuliform corollas; white versus pink corollas; scented versus non-scented corollas; orange markings versus no markings on corolla mouth; long exserted versus inserted stamens, five calyx lobes versus two calyx lobes, paired versus single flowers, four versus six episepals, loose versus compact inflorescences. Characters were nevertheless randomly distributed within species complexes such as *Abelia forrestii* with five sepals instead of two or *Abelia uniflora* with a variable number of sepals. A few apomorphic characters were also identified such as the inflated mouth corolla in *A. schumannii* (Table 3, Figs. 6 & 7).

Nomenclature of taxa

see appendix 2

Key

see appendix 3

Distribution

Abelia is widely distributed across much of China. Its range is restricted in the north by the Qin Ling Range, in the west by the deep valleys of the Qinghai-Tibetan plateau (QTP), in the east by the East China Sea reaching the Ryukyu Islands and to the South reaching the Mountains of Northern Vietnam. The species are distributed in a wide array of habitats (roadside, woodlands, and scrublands) restricted to mountains, deep valleys and hills gradually diversifying from West to East. Most taxa are widespread with overlapping ranges, but some can be localised and with restricted ranges (Fig. 8).

- *Abelia forrestii* var. *forrestii* is restricted to one locality in the Nujiang valley.
- *Abelia forrestii* var. *gracilenta* is restricted to the first bend of the Yangtze River in the Leaping Tiger Gorge.
- *Abelia macrotera* var. *zabelioides* is confined to E'mei Shan but intermediate forms are more widespread.
- *Abelia macrotera* var. *parvifolia* is only recorded from around Yichang in Hubei.
- *Abelia macrotera* var. *myrtilloides* has a small range in northern Sichuan.
- *Abelia chinensis* var. *achersoniana* is only found in Hong Kong and may be a coastal ecotype.
- *Abelia chinensis* var. *lipoensis* can be found in Southern Yunnan, Guizhou, Guangxi and Guangdong.
- *Abelia chinensis* var. *hanceana* grows in Fujian: Xiamen and also Taiwan as well as the Ryukyu Islands.
- *Abelia uniflora* grows in Fujian, Jiangxi, Anhui and Zhejiang

Cultivars

The breeding of *Abelia* only started in 1950 more than 50 years after the discovery of the hybrid *Abelia* x *grandiflora*. The origin of *Abelia* x *grandiflora* has been documented by Ed. André (1886) 'Seen in the M.M. Rovelli Brothers Nurseries in Pallanza (Lake Maggiore); grown from a seedling a few years ago this shrub, that MM. Rovelli named (*A. rupestris grandiflora*) is more vigorous with more persistent leaves, ovate, serrate, glossy green and with large tubular flowers, fragrant, pinkish rose, blooming during all seasons, in full sun'.

Its morphology strongly suggests it is of hybrid origin between *A. chinensis* R.Br. (syn: *Abelia rupestris* Lindl.) and *Abelia uniflora*. The morphological characters are intermediate between the two parents. Flowers are axillary or in small cymes, single and with 4 episepals similar to *A. uniflora*. The flowers are white, fragrant, infundibuliform-campanulate and slightly bilabiate, the stamens are slightly exserted and therefore intermediate between the two parents. The leaves are more similar to *A. chinensis* (Table 4, Figs. 9 & 10).

For several decades breeding was focused on obtaining yellow, variegated leaves as well as dwarf variants. Recent breeding has focused on new hybridisation including *A. schumannii* and *A. chinensis* var. *chinensis* and the creation of several backcrosses that are of interest in this study. Amongst them we can cite 'Saxon Gold', and 'Rose Creek'. The first backcross recorded nevertheless predates this recent activity and 'Edward Goucher', one of the most popular cultivars, was obtained in 1911. Michael Dirr has been an active participant in most breeding programs at the University of Georgia (Dirr, 2009).

'Francis Mason' was obtained in 1950 in the Mason nurseries, New Zealand. It is by far the most commonly grown cultivar of *Abelia* x *grandiflora* and is distinguished by its yellow variegated leaves often reverting to all yellow or green. Another origin of *A.* x *grandiflora* cultivars is 'Sherwood' published in the Proceedings at the annual meeting of the American Association of Nurserymen, Florists and Seedsmen 1949:123, it has a more compact habit. A few variegated forms have also been obtained from 'Sherwood'. See Table 5 for list of hybrids and cultivars with their breeding history.

Morphological characters

Morphological variation between cultivars was paralleled with the variation in wild taxa and could mostly be attributed between two character states such as glossy versus non glossy leaves; bilabiate versus infundibuliform corollas; white versus pink corollas; scented versus non scented corollas; long exserted versus inserted stamens, five calyx lobes versus two calyx lobes, paired versus single flowers, four versus six episepals, loose versus compact inflorescences. Characters were randomly distributed within hybrids and backcross such as *Abelia* 'Saxon Gold' with five sepals instead of two or *Abelia x grandiflora* with a variable number of sepals. A few apomorphic characters were also identified such as the variegated leaves or corolla spur in *Abelia* 'Sherwood' (Table 4, Figs. 9 & 10).

DISCUSSION

Abelia is a typical genus of the Sino-Japanese Floristic Region (SJFR) (Qiu *et al.*, 2011). The QTP is the highest and largest plateau in the world and is regarded as a biodiversity hotspot where deep valleys have allowed for many species to occur sympatrically, however hybridisation and introgression are common problems for species delimitation (Xu *et al.*, 2010; Liu *et al.*, 2013). A clear West-East distribution pattern can be observed with *A. macrotera* var. *mairei* in the most western part (Yunnan, Hengduan Mountains). *Abelia schumannii* is restricted to the deep valleys of the QTP. *Abelia forrestii* is the most localised species and restricted along the Salween-Mekong divide (Nujiang River (Salween) for var. *forrestii* and the first bend of the Yangtze River for var. *gracilenta*). *Abelia chinensis* is distributed in a wide area in eastern China as well as more isolated populations in Hubei and Sichuan. *Abelia chinensis* diversifies at the contact of *Abelia macrotera* and *A. uniflora* with *A. chinensis* var. *lipoensis* in South Yunnan, Guangxi and Guizhou and *A. chinensis* var. *hanceana* in Xiamen, Taiwan and the Ryukyu Islands. Finally, a clear disjunction can be observed between *A. uniflora* in Anhui, Fujian, Jiangxi and Zhejiang with *Abelia macrotera* in Hubei and further west; this seems to be linked with the dominance of *A. chinensis* in Jiangxi, Hunan and Guangxi. A north-south distinction can be observed with *A.*

macrotera var. *deutziaefolia* occurring in Yunnan and Guangxi which may also been driven by the presence of *A. chinensis* in the same area (Fig. 8).

Possible phylogeographic events cited from the literature:

1. *Abelia macrotera* - *Abelia uniflora* west-east disjunction with allopatric incipient speciation (Qiu *et al.*, 2009a)
2. *Abelia schumannii* range expansion from SE plateau edge onto eastern QTP platform (Yang *et al.*, 2008)
3. *Abelia forrestii* glaciation survivor east and west of the Mekong-Salween divide (Li *et al.*, 2011)
4. *Abelia macrotera* var. *deutziaefolia* and *A. chinensis* var. *lipoensis* genetic differentiation among isolated populations from Guangxi. Guangdong, Hunan and Hainan; localized range expansion, possibly during interglacial periods (Tian *et al.*, 2010)
5. *Abelia chinensis* var. *hanceana* ancient allopatric-vicariant segregation across Japan vs. eastern China (Qiu *et al.*, 2009b)

Abelia macrotera – Abelia uniflora: Hybridization and introgression with *Abelia chinensis*

Abelia uniflora is the most enigmatic species in the genus *Abelia*, it was only briefly described (Wallich, 1829) and was the first taxon to be introduced into cultivation (as early as 1845 by Robert Fortune). It was illustrated in the *Curtis Botanical Magazine* (Hooker, 1853) and is likely to have become extinct in cultivation after this date. *Abelia* x *grandiflora* is said to have been obtained in Italy by MM. Rovelli Brothers Nurseries in Pallanza (Lake Maggiore) as a cross between *Abelia chinensis* and *A. uniflora* (André, 1886).

The ITS sequence analysis (Fig. 2) shows that *Abelia uniflora* forms a clade with *A*. x *grandiflora* (BP 91/ PP 1, Fig. 2) but the position is unresolved alongside *A. macrotera* in the cpDNA analysis. This is an indication of the hybrid origin of cultivated *Abelia* x *grandiflora* involving *A. uniflora* as one progenitor but the other progenitor is not identified definitively. It may be *A. chinensis* as stated in the literature or *A. macrotera* as indicated (albeit weekly) in the phylogenetic analysis or even a hybrid individual between the two (*A. chinensis* and *A. macrotera*) as the other progenitor.

The AFLP study fails to resolve this issue because it does not indicate any admixture in the *Abelia* x *grandiflora* (Fig. 5); this suggests that *A. uniflora,* which was not sampled in the AFLP study, is probably the paternal parent. A lack of signal indicating the hybrid origin of *A*. x *grandifolia*, in the Structure analysis, is intriguing given the phylogenetic evidence but the involvement of *A. uniflora* will need to be determined conclusively in subsequent genetic studies.

A clear disjunction between *A. uniflora* and *A. macrotera* can be observed (Fig. 8), which is mainly due to its habitat requirements such as higher elevation for *A. macrotera* but also because *A. chinensis* forms an introgression barrier between *A. macrotera* in the west and the relictual zone of *A. uniflora* in the east. This is corroborated by its morphology which is similar to *A*. x *grandiflora* (Figs. 7 & 10):

- Variable number of sepals 2-4.
- Infundibuliform-bilabiate white corolla, with faint markings on lower lip.
- Slightly exserted stamens.

This study highlights the genetic distinction between *A. uniflora* and *A. macrotera*, two taxa that are often difficult to identify based on their morphology alone (Table 3, Figs. 6 & 7). The identity and origin of *A*. x *grandiflora*, a hybrid between *A. chinensis* and *A. uniflora* is weakly supported and *Abelia uniflora* shows evidence of allopatric speciation due to hybridisation and introgression between *A. macrotera* and *A. chinensis.*

***Abelia schumannii*, hybridization in sympatric zones**

Abelia schumannii was introduced in cultivation after *A. uniflora* (Edinburgh collection Wilson E.H. 1230 collected in July 1908 in Sichuan, Wenchuan Xian). *Abelia schumannii* is now the only commonly available species of *Abelia* in the horticultural trade, and has been used in most selection programs.

Abelia 'Edward Goucher' is the hybrid *A.* x *grandiflora* x *schumannii*, obtained at Glenn Dale Plants, USA, in 1911. This is one of the oldest cultivars created and it is still commonly grown in the USA but it is much less frequent in the rest of the world. *Abelia* 'Edward Goucher' sepals are two and one is often notched at the apex, the corolla is similar to *A. schumannii* but the style is often exserted and the leaves are glossy adaxially. In its morphology it is similar to *A. uniflora* except the dark purple-pink corolla and glossy leaves (Figs. 9 & 10).

Abelia 'Edward Goucher is identified as a hybrid in the AFLP study with admixture from *A. schumannii* and *A.* x *grandiflora* (Figs. 3--5).

Abelia 'Maurice Foster' was collected by Maurice Foster in Sichuan probably around Luding and was grown by Liss Forest Nurseries (UK). *Abelia* 'Maurice Foster' leaves are leathery, glossy adaxially and with prominent teeth on the margin and an acuminate apex. Flowers appear in short cymes or in clusters, with a purplish-pink corolla that has an inflated mouth. It superficially resembles *A. macrotera* var. *macrotera* but the leaves are smaller and the corolla mouth is more inflated (Fig. 6). The area where it was collected is covered by both *A.*

macrotera var. *zabelioides* and *A. schumannii* and many herbarium specimens from the same area have intermediate characters between the two taxa.

Abelia 'Maurice Foster' admixture was identified in STRUCTURE between *A. macrotera* and *A. schumannii* (Fig. 5). We can infer that hybridization, in sympatric regions of Sichuan, is common between taxa.

The AFLP study revealed that *Abelia schumannii* is a distinct species (Figs. 3 & 4) which was unexpected because the morphology is similar to *A. macrotera*. Its wide tube abruptly flaring to the corolla mouth is one of the most striking characters and probably linked to a specialized pollination syndrome and its distribution in the deep valleys of the QTP.

Backcrosses between closely related taxa such as *A. macrotera* and *A. schumannii* creates a similar effect to introgression but have a different morphological signature (Figs. 6 & 7):

- Leaves adaxially glossy.
- Number of sepals 2 with one notched apically.
- Bilabiate, inflated and purplish pink corolla with orange markings on lower lip.
- Inserted stamens, slightly exserted style.

***Abelia forrestii* limited introgression and gene infiltration**

Abelia forrestii is the most localised taxon of *Abelia* only occurring in two localities within two of the deepest valleys of China. With its five sepals, long tubular-infundibuliform corolla, white-pink corolla without markings and fragrant flower it is one of the most distinct taxa in the genus (Figs. 6 & 7).

Abelia 'Saxon Gold' is also one of the more unusual cultivars obtained with its 5 sepals, biliabiate, purplish pink corolla without markings and yellow leaves (Figs. 9 & 10).

In the STRUCTURE analysis *A.* ‘Saxon Gold’ shows an admixture between *A.* x *grandiflora* and *A. schumannii*, indicating a backcrossed origin (Fig. 5). In the same analysis one individual of *A. forrestii* shows a small admixture with *A. macrotera*. It seems that the two taxa have a similar origin and that the isolation of *A. forrestii* within the deep valleys of the Nu-Jiang (Salween) and Yangtze Rivers allowed for limited introgression followed by allopatric speciation. Their morphological signatures are similar:

- Number of sepals 5.
- Infundibuliform pinkish white and scented corolla without markings on lower lip.
- Slightly exserted stamens and style.

Abelia macrotera var. deutziaefolia and A. chinensis var. lipoensis ***chloroplast capture***

Abelia macrotera var. *deutziaefolia* is distributed is southern Yunnan, Guangxi and Guizhou provinces (Fig. 8). It has stems which are densely pubescent, its purple corollas have faint markings and have a short tube, the style is slightly exserted and the sepals are obtuse (Figs. 6 & 7).

Abelia ‘II6306’ is an experimental hybrid sent by Liss forest Nursery (UK) it resembles *A. chinensis* but its inflorescence are loose and corollas are bilabiate-infundibulform as in *A.* x *grandiflora* (Fig. 10).

In the STRUCTURE analysis *A.* ‘II6306’ shows admixture between *A.* x *grandiflora* and *A. chinensis*, indicating a backcrossed origin (Fig. 5).

Organellar DNAs (i.e., chloroplast DNA and mitochondrial DNA) can be used for tracing the long-term effects of hybridization in natural populations. Because their inheritance is uniparental, groups of associated loci are not separated by recombination, so that a great deal of historical information is preserved in these sequences (Whittemore and Schaal, 1991). As seen in the Bayesian tree of *Abelia* based on the combined *rbc*L, *trn*L-F and *mat*K sequence data (Fig. 1), *Abelia* x *grandiflora, Abelia chinensis* and *A. macrotera* var. *deutziaefolia* form a polytomy (BP 54/ PP 0.96). Hybridization followed by introgression between *A. chinensis* and *A. macrotera* can therefore be hypothesised.

Abelia macrotera var. *deutziaefolia* and *Abelia chinensis var. lipoensis* both share a similar distribution range in southern Yunnan, Guizhou and Guangxi where both species *Abelia macrotera* and *Abelia chinensis* grow sympatrically. *Abelia* 'II6306' and *Abelia chinensis* var. *lipoensis* show a similar loose inflorescence as well as other morphological characters associated with *A. macrotera* (Fig. 7):

- Number of sepals 5.
- Loose inflorescence.
- Glabrous stems.
- Infundibuliform-bilabiate and white corollas.
- Stamens exserted.

Abelia macrotera var. *deutziaefolia* is on the other end of the spectrum, being introgressed from *A. chinensis* and sharing a few similar morphological characters (Figs .6 & 7).

- Number of sepals 2.
- Bilabiate purplish pink corolla with faint orange markings on lower lip.
- Inserted stamens, slightly exserted style.

Abelia chinensis var. hanceana segregation across Japan vs. eastern China

Abelia chinensis var. *hanceana* is distributed in Xiamen and Taiwan, China as well as the Ryukyu Islands but not reaching Kyushu, Japan. This variety is characterised by its smaller size and compact inflorescences. Its leaves have a crenate margin and resemble leaves of *Abelia uniflora* (Figs. 6 & 7).

Abelia 'Rose Creek' is a backcross *A.* x *grandiflora* x *A. chinensis* and resembles *Abelia chinensis* but it has more compact inflorescences (Figs. 9 & 10).In the STRUCTURE analysis *A.* 'Rose Creek' also showed admixture between *A.* x *grandiflora* and *A. chinensis* indicating a backcrossed origin (Fig. 5). The Okinawa trough and associated straits began to rift at 1.55 Ma, isolating the Ryukyu Islands from the Chinese continent, Japanese islands, Taiwan Island and some of the islands from each other. Physical isolation began to generate the allopatric speciation within these islands (Osozawa *et al.*, 2015). Vicariance of *Abelia chinensis* var. *hanceana* across the East China Sea between Xiamen, Taiwan and the Ryukyu Islands may have favoured limited backcrossing along the eastern edge of *Abelia chinensis* range.

Some characters shared are (Fig. 7):

- Number of sepals 5.
- Compact inflorescence.
- Infundibuliform, white corollas.
- Stamens long exserted.

Hybridization-backcrossing driven speciation

We have highlighted the diversity of the genus and clarified the status of some of the most controversial names. The confusion between names is probably due to the complex evolutionary histories between taxa, the principal forces being hybridization and introgression. Breeding in horticulture has merely reproduced natural processes that occur in longer time scales and has been blurred by introgression. Character infiltration due to back crossing is well known to horticulturists and is one of their major aims, this phenomenon also provides an evolutionary advantage that leads to novel adaptations and cryptic taxa. Some of the infiltrated characters are here identified (Table 6, Fig. 11):

- Calyx lobe numbers 2, 2-5 or 5
- Inflorescence compact or loose
- Leaves glossy adaxially.
- Stems glabrous.
- Corolla bilabiate, infundibulform or bilabiate-infundibulorm or inflated.
- Flowers white, pinkish purple with or without orange markings.
- Flower scented.
- Exserted stamens and style.

Abelia 'Edward Goucher' has a similar origin to *A.* 'Saxon Gold' but exhibits very different characters only having two sepals a bilabiate purplish-pink corolla with strong markings and an exserted style. This demonstrates that recombination during hybridisation is random and can produce new combinations of genes which in turn can increase the morphological diversity and result in novel characters belonging to different species. Sepal number, corolla shape and inflorescence structure are amongst these easily identifiable characters in *Abelia* that could be transferred between taxa. The establishment of new intraspecific taxa is a frequent outcome of introgression; backcrossing to one or both parents leads to the infiltration of specific genes from one species to another (Fig. 11). Such interspecific gene-flow, known as introgression, results in the production of offspring that are clearly referable to one of the parent species, but that possess certain characters inherited from the second species. Sometimes these products may become stabilised and develop into a new intraspecific taxon or cryptic species (Abbott, 1992).

Several cryptic taxa are here identified (Table 6):

- *Abelia chinensis* backcrosses with: *A. chinensis* var. *hanceana* (possibly with *A. uniflora*) and var. *lipoensis* (possibly with *A. macrotera* var. *macrotera*) / *Abelia* 'Rose Creek', *Abelia* 'II6306'.
- *Abelia uniflora* s.l. backcrosses with: *A. macrotera* var. *deutziaefolia* and *A. uniflora*, *A. forrestii* / *Abelia* 'Edward Goucher', *Abelia* 'Saxon Gold'.

Backcrossing does not necessarily occur exclusively between two taxa and can involve many taxa belonging to the same complex such as the *A. uniflora* species complex and *A. chinensis*. This is less likely in the wild because it requires taxa to be growing sympatrically.

CONCLUSIONS

'It appears to be necessary to accept that some taxa are highly variable in the wild and that, consequently, some names in common use in the West merely represent points in a continuous spectrum of variation of what is better regarded as a single species' Barnes, P (2001). Our aim was to bridge the gap between horticulturalists and the botanical community in order to understand the genetic diversity within *Abelia* and where to concentrate efforts into conserving and exploiting the benefits offered by ornamental plants. A clearer view of the taxonomy, speciation mechanisms and morphology is here presented and highlights the importance of hybridization and backcrossing in breeding programs and also in natural speciation. It is not surprising that with these types of complex and multidirectional processes, taxa of *Abelia* are often difficult to identify and the species boundaries are blurred. The knowledge of the genetic diversity and genetic relatedness within *Abelia* is potentially useful to improve the current strategies in breeding and germplasm conservation to enhance the ornamental and economic value of the genus. An understanding of both the genetic diversity and the population structure of *Abelia* in China can also provide insight into the conservation and management of some endangered taxa.

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Table 1. Statistics of the three regions used

	ITS	*rbcL*	*trnL-F*	*matK*	CpDNA Combined
No. taxa	18	24	24	24	24
Total aligned characters	637	604	849	779	2232
Constant characters	572	541	736	634	1911
Parsimony informative	40	61	52	76	153
Consistency index	0.814	0.57	0.923	0.889	0.833
Retention index	0.91	0.484	0.945	0.923	0.865
Evolution model	GTR+G	HKY+G	GTR+G	GTR+G	-

Table 2. Statistics of the AFLP analysis

	G13 nr.	G13 %	G2 nr.	G2 %	Y15 nr.	Y15 %
Initial bin number	149.00	100	166.00	100.00	173.00	100.00
Final bin number	76.00	51.01	111.00	66.87	113.00	65.32
Removed low intensity	49.00	32.89	44.00	26.51	50.00	28.90
Removed non replicable bin	21.00	14.09	8.00	4.82	10.00	5.78
Removed rare Frequency bin	3.00	2.01	3.00	1.81	0.00	0.00
Error rate bin	0.0658	0.00	0.0360	0.00	0.0487	0.00
Ibin	0.2824	0.00	0.2666	0.00	0.2485	0.00

Table 3. Morphological characters of the five species of *Abelia*

Characters	***Abelia chinensis***	***Abelia* schumanii**	***Abelia uniflora***	***Abelia macrotera***	***Abelia forrestii***
Corolla shape	infundibuliform-campanulate	bilabiate with inflated mouth	bilabiate with inflated mouth	bilabiate	tubular-infundibuliform
Corolla colour	white without markings	purplish-pink with orange markings	white-Purplish with faint yellow markings	purplish-pink with orange markings	purplish-pink without markings
Fragrance	scented	Non-scented	?	Non-scented	scented
Bloom	Sept--Dec	May--Sept	May--Sept?	May--Sept	May--Sept
Anthers and style	long exserted	inserted	inserted to exserted	inserted to slightly exserted	inserted to slightly exserted
Calyx lobes	5	2	2--4	2	5
Flowers	paired	single	single	single	single
Epicalyx bracts	6	4	4	4	4
Inflorescence	terminal, flowers many and cymose	flowers few axillary	flowers few axillary	flowers few axillary	flowers few axillary

Table 4. Morphological characters of the cultivated species of *Abelia*

Key characters	***Abelia chinensis***	***Abelia* x *grandiflora***	***Abelia uniflora***	***Abelia schumannii***
Leaves	glossy adaxially	glossy adaxially	?	not glossy
Leaves	semi-evergreen	semi-evergreen	?	deciduous
Corolla shape	infundibuliform-campanulate	infundibulform-bilabiate	bilabiate	bilabiate
Corolla colour	white without markings	purplish-pink with orange markings	white-pink with faint yellow markings	purplish-pink with orange markings
Fragrance	scented	scented	?	non scented
Bloom	autumn	summer-autumn	summer	summer
Androecium	long exserted	inserted to exserted	inserted	inserted
Style	long exserted	slightly exserted	slightly exserted	inserted
Calyx	5	2--5	2--4	2
Flowers	paired opening consecutively	single	single	single
Epicalyx	6	4	4	4
Inflorescence	terminal compact	loose to compact	loose	loose

Table 5. List of *Abelia* Cutivars names and descriptions.

Cultivars name	Preferred selling name/ synonyms	Breeder	Date	Parentage	Description
'Abghop'	**HOPLEYS**	Hopleys Nurs.	1992	'Francis Mason' Sport	Dwarf, variegated leaves, teratological white flowers.
'Bumble Bee'		?	?	*Abelia schumanii*	Selection with larger flowers.
'Canyon Creek'		Dirr, M.	2002	*A. chinensis* x *A.* x *grandiflora*	Sepals 4--5, corolla infundibulifrom-bilabiate pink without markings, style and stamens not exserted inflorescence not dense terminal leaves green, glossy.
'Compact'	'Compacta'	?	?	similar to 'Sherwood'	The white flowers have a basal spur at the base like the rest of the 'Sherwood' group.
'Conti'	**CONFETTI**	Flowerwood Nurs.	1987	Sport of 'Sherwood'	Variegated dwarf form with teratological flowers.
'Edward Goucher'	'Dwarf'	Glenn Dale Plants	1911	*A.* x *grandiflora* x *schumanii*	Flowers single, bilabiate, axillary dark purple. Sepals 2 often notched at the apex. Leaves glossy.
'Francis Mason'		Mason nursery New Zealand	1950 or 1970	*A.* x *grandiflora* selection	Variegated form of *A.* x *grandiflora*. Copper coloured young shoots. Leaves variegated yellow or yellow margined.
'Goldenglossy'	**GOLD DUST**	Jerry Brunson.		Sport of 'Sherwood'	Compact with yellow variegated leaves.
'Goldspot' group	'Aurea', 'Gold Sport'…			Selections of *A.* x *grandiflora* 'Francis Mason'	With more stable and less reversion or more yellow variegation.
'Kaleidoscope'		Plant Haven Inc.	1997	Sport of A. 'Little Richard'	Dwarf, leaves with cream yellow and orange variegation.
'Keiser'	**RUBY ANNIVERSARY**	Susan Keiser	1999	Back cross chinensis	Not so compact inflorescences. Sepals 4--5, corolla infundibulifrom white without markings, style and stamens exserted leaves green, glossy.
'Lavender Mist'		University of Georgia	2006	*A.* 'Edward Goucher' x *Abelia chinensis*	Heavy bloomer, with clusters of fragrant lavender flowers. Sepals 5 reddish. (HortScience 41:967-1084 (2006)
'Little Richard'		Currin's nursery	?	Sport of 'Sherwood'	Lustrous dark green leaves. Large flowers, corolla whitish with 1--2 spurs at the base of the corolla, typical of Sherwood group.
'Lynn'	**PINKY BELLS**	Spring meadow Nursery	2003	*Abelia* 'Bumblebee' x *A.* 'Little Richard'	Compact plant with large pendulous, lavender-pink flowers. Sepals mostly 2, corolla almost infundibuliform pink with large broad mouth, markings faint.

‘Mardi Gras’		Crowder Rick	2003	*Abelia* x *grandiflora* x *chinensis* sport	Leaves green with white and pink variegated margins.
‘Maurice Foster’		Liss Nursery ex. 19770008	1977	*Abelia macrotera* x *A. schumanii*	Collected by Maurice Foster in Sichuan (probably Luding). Inflorescence in short axillary raceme, sepals narrow with acute apex, Leaves leathery.
‘Mei-fu-hana-tsukubane-utsugi'		Suda, H. 1976. Variegated plants :180	1972	Irradiated *A.* x *grandiflora*	Yellow margined and blotched leaves. Obtained by gamma-rays.
‘Minduo1’	**SUNNY ANNIVERSARY**	Olivier Nazeyrollas, Beaufort en Vallee.	2005	A. x grandiflora ‘Minfest’ x unknown	Sepals mostly 2, corolla almost infundibuliform pink with large broad mouth, markings strong reaching base of corolla tube. Style exserted.
‘Panache’ or **‘Panash’**	‘Silver Panache’			*A* x *grandiflora* 'Prostrata'	Stable variegated leaves, silver to yellow margined. Prostate, Flowers teratological like 'Conti'.
‘Pleasant Surprise’		Pleasant View Nurs.	2002	*A.* x *grandiflora* x *chinensis.*	(Hort Science 38(6): 1300. 2003). Flowers single, sepals 5, corolla infundibuliform-bilabiate, pinkish white, sepals obovate, Inflorescence dense.
‘Plum Surprise’		University of Georgia	2006	*A.* 'Edward Goucher' x *A.* 'Francis Mason'	(HortScience 41:967-1084 (2006) Sepals 4-5, Corolla bilabiate white-pink with faint markings. Leaves small moderately glossy and green.
‘Prostrate White’	‘Prostrata’	Abbott, D.	1955	Similar to *A.* ‘Sherwood’	Similar to *A.* ‘Sherwood’ but more prostrate.
‘Radiance’		Plant Haven Nurs.	2006	*A.* ‘kaleidoscope’	Variegated compact sport.
‘Raspberry Profusion’		University of Georgia	2006	*A.* 'Edward Goucher' x *Abelia chinensis*	(HortScience 41:967-1084 (2006)). Very heavy bloomer. Panicles are large and showy with fragrant pink flowers and raspberry-colored sepals.
‘Rika 1’	**BRONZE ANNIVERSARY**	Grand Haven	2003	*Abelia* x *grandilora* ‘Minipan’	Young leaves with bronze colour, similar to ‘Francis Mason’.
‘Rose Creek’		Dirr, M.	2001	*A. chinensis* x *A.* x *grandiflora*	Sepals 5, corolla infundibuliform white, style and stamens exserted inflorescence very dense terminal leaves glossy.
‘Saxon Gold’		Saxon Nurs.	1997	*Abelia schumanii A.* x *grandiflora*?	This is a very intriguing cultivars, flowers and inflorescence are like *Abelia schumanii* but differs in having 5 sepals and golden yellow foliage.

'Sherwood' or **'Sherwoodii'**	Published as 'Sherwoodi'.		1935	Sport of *A*. x *grandiflora*	American Assoc. Nurs. Proc. 1949:123. Very compact.
'Short and Sweet'		Robert Pearce	2000	*A*. x *grandiflora* 'Compacta'	(Plant Variety journal 14(1):15.2001). similar to *A*. 'Conti'.
'Sunrise'		Taylor's nursery NC, USA	1996	*A* x *grandiflora* mutation	Smaller but not as 'Conti'. Leaves yellow margined to cream orange or red margined, stem dark red. Teratological flowers.
'White Marvel'		Sakaue; Katsuya, Hines Nurs.	2000	*A*. x *grandiflora* 'Francis Mason'	New shoots and foliage which emerge white, cream, pale yellow to gold with occasional terminal golden orange foliage.

Table 6. Morphological character changes paralleled between cultivars and wild taxa.

\+ introgression -   - introgression +

	Backcross '*uniflora*'	Backcross '*uniflora*'	Hybrid	Backcross *chinensis*	Backcross *chinensis*
Sepals	2	2--3	2--5	4--5	5
Epicalyx	4	4	4	4 or 6	6
Flower	single	single	single	single-paired	paired
Inflorescence	loose	loose to compact	loose to compact	loose	dense
Corolla	bilabiate	infundibuliform-bilabiate or bilabiate	infundibuliform-bilabiate	infundibuliform-bilabiate or infundibuliform-campanulate	infundibuliform-campanulate
Fragrance	non-scented	scented or non-scented	scented	scented	scented
Bloom	summer	summer-autumn	summer-autumn	summer-autumn	autumn
Androecium and style	inserted	inserted to exserted	inserted to exserted	inserted to exserted	long exserted
Wild taxa	*A.uniflora*	*A.forrestii*		*A. chinensis* var. *lipoensis*	*A.chinensis* var. *hanceana*
Cultivated taxa	A.'Edward Goucher'	A.'Saxon Gold'	A.x grandiflora	A.'II6306'	A.'Rose Creek'

Figure 1. Bayesian tree of *Abelia* and outgroups based on the combined *rbc*L, *trn*L-F and *mat*K sequence data. MP (first), bootstrap branch support and Bayesian posterior probabilities (last) indicated above a cut-off value of 50 and 0.5, respectively.

Figure 2. Bayesian tree of *Abelia* and outgroups based on the Internal Transcribed Spacer (ITS) sequence data. MP (first), bootstrap branch support and Bayesian posterior probabilities (last) indicated above a cut-off value of 50 and 0.5, respectively.

Figure 3. Neighbour Joining Tree of 29 *Abelia* cultivars and taxa based on AFLP analysis with three pair primer combinations

Figure 4. Principal coordinates analysis based on the distance between individual amplified fragment length polymorphism (AFLP)

Figure 5. STRUCTURE analysis of *Abelia* cultivars and taxa (K=2, 4 and 5)

Figure 6: Photographs of *Abelia* taxa. A--B. *Abelia macrotera* var. *deutziaefolia* from Guizhou, Guiyang note the short thick tube and exserted style*;* C. *Abelia uniflora* cultivated in Wuhan B.G. note the white corolla and faint yellow markings; D & G. *Abelia chinensis* var. *chinensis* cultivated at Kew, note the campanulate corolla and long exserted styles and stamens; E. *Abelia forrestii* var. *forrestii* from Yunnan, Nujiang, note the long tubular, infundibuliform corolla without markings; F. *Abelia macrotera* var. *mairei* from Yunnan, Kunming; H. *Abelia schumanii* cultivated, note the large and wide corolla mouth; I. *Abelia macrotera* x *A. schumanii* 'Maurice Foster' cultivated; J. *Abelia macrotera* var. *macrotera* from Sichuan, Bazhong.

Figure 7: Line drawings illustrating key morphological characters of *Abelia* taxa. A. Flowers in lateral views; B--G. *Abelia forrestii* var. *forrestii*; B. corolla; C. Nectary bulge; D. Corolla mouth; E. Longitudinal section of the corolla; F. Androecium; G. Style; H. Flowering branches; I. Epicalyx and achenes; J. Habit; K--M & O--P. *Abelia macrotera* var. *deutziaefolia*; K. Stem node indumentum; L. Adaxial leaf, M. Abaxial leaf; N. *Abelia chinensis* var. *hanceana* adaxial leaf; O. Abaxial leaf surface; P. Adaxial leaf surface.

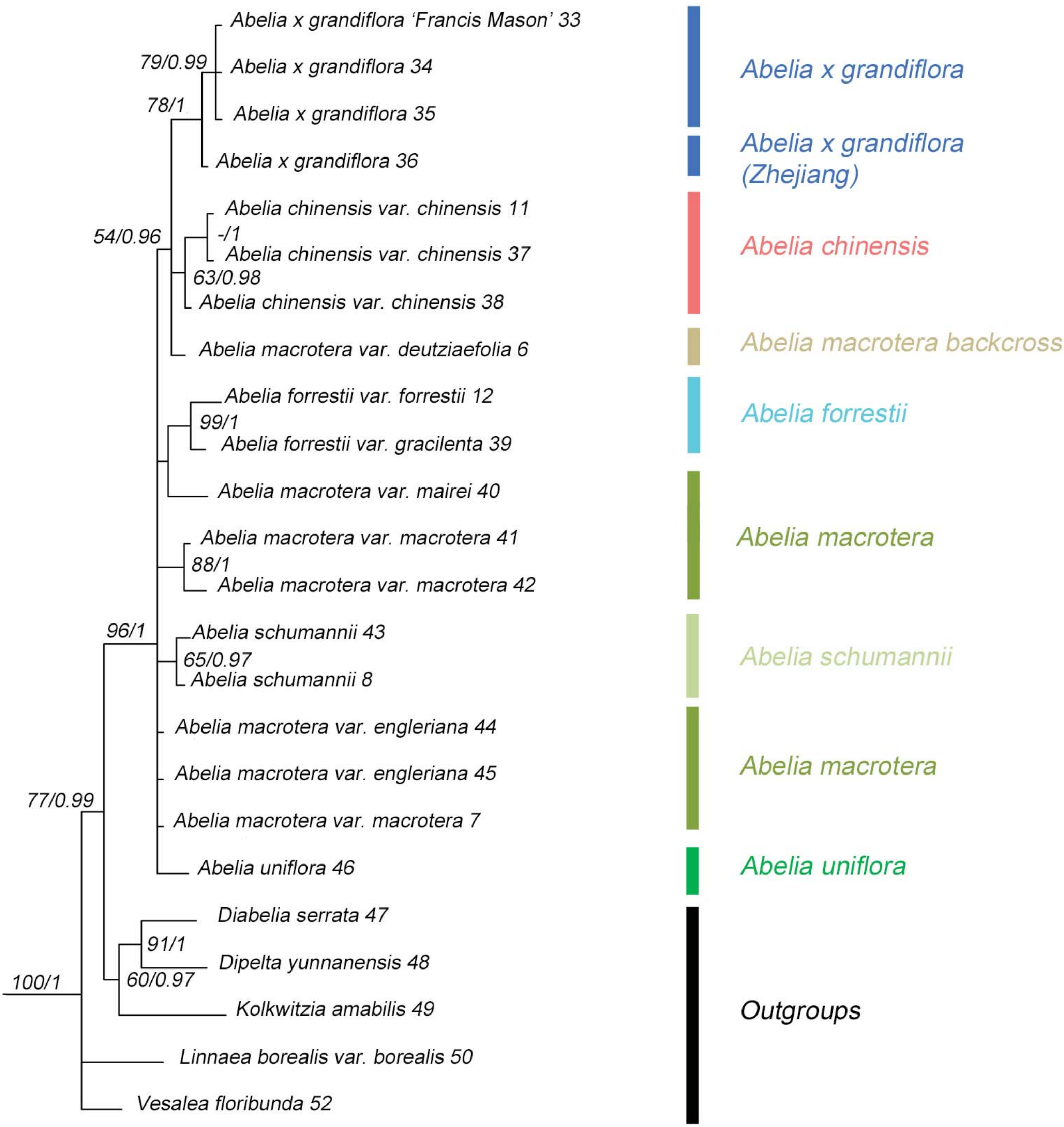
Figure 8: Distribution map of *Abelia* taxa drawn from herbarium specimens using BRAHMS and DIVA GIS. Map obtained from 761 collections.

Figure 9: Photographs of *Abelia* cultivars at the RHS Wisley trial garden A--B. *Abelia* 'Edward Goucher' note the two sepals and the notched apex; C--D. *Abelia* 'Saxon Gold' note the five sepals and yellow leaves; E--F. *Abelia x grandiflora* 'Francis Mason'; G. *Abelia x*

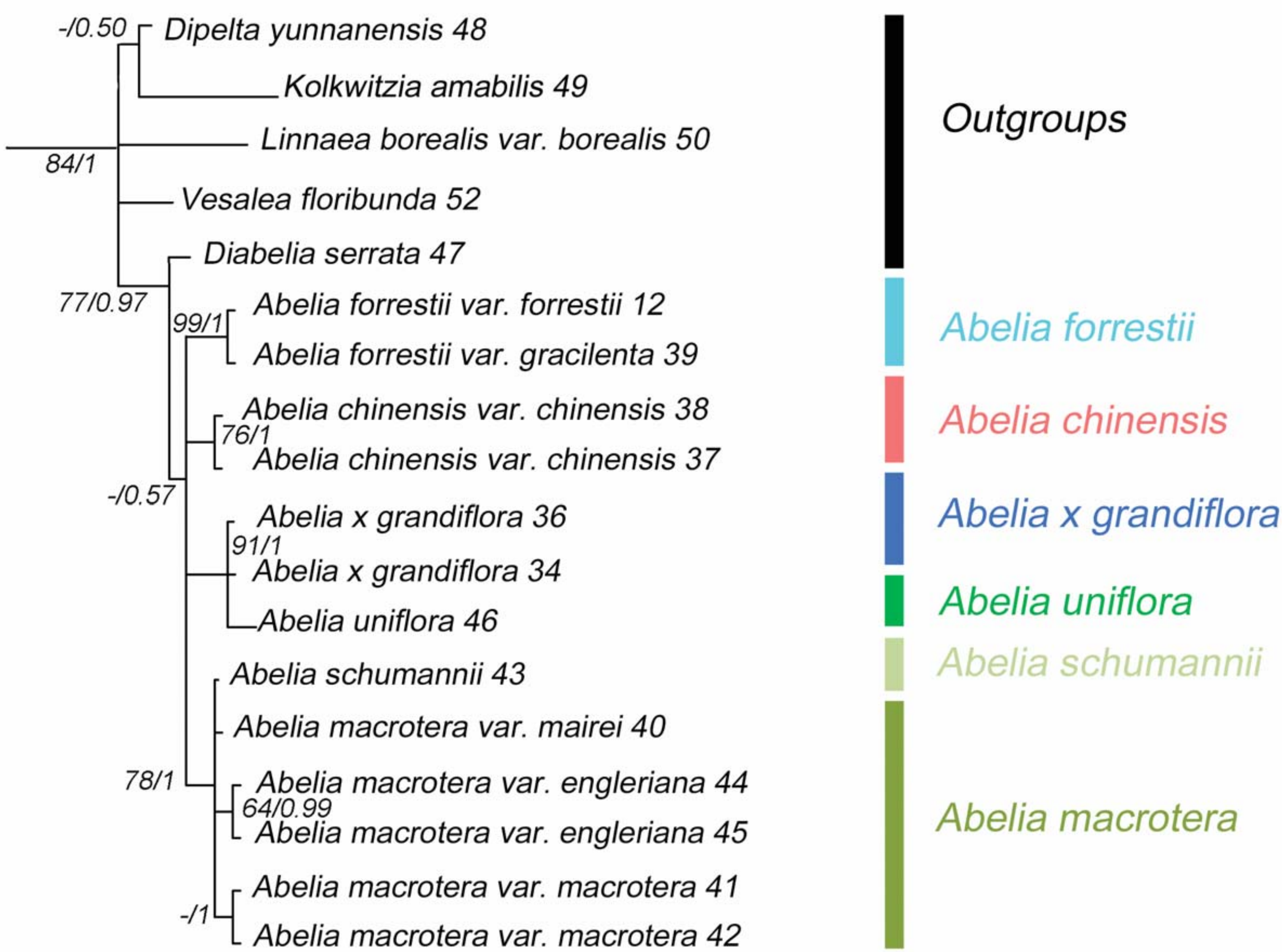
grandiflora ‘Conti’ note the variegated leaves; H. *Abelia x grandiflora* ‘Sherwood’ note the basal spur on the corolla; I--J. *Abelia* ‘Pleasant Surprise’; K. *Abelia* ‘Rose Creek’ note the dense terminal inflorescence and campanulate corolla.

Figure 10: Line drawings illustrating key morphological characters of *Abelia* cultivars. A. Flowers in lateral views; B--G. *Abelia x grandiflora* ‘Francis Mason’; B. corolla; C. Nectary bulge; D. Corolla mouth; E. Longitudinal section of the corolla; F. Style; G. Androecium; H. Flowering branches; I. Epicalyx and achenes; J. Habit; K--O. *Abelia x grandiflora* ‘Francis Mason’; K. Stem node indumentum; L. Adaxial leaf, M. Abaxial leaf; N. Abaxial leaf surface; O. Adaxial leaf surface.

Figure 11: Principal coordinates analysis based on the distance between individual amplified fragment length polymorphisms (AFLPs) plotted with two of the main diagnostic characters for the genus: sepal number and inflorescence with single or paired flowers.

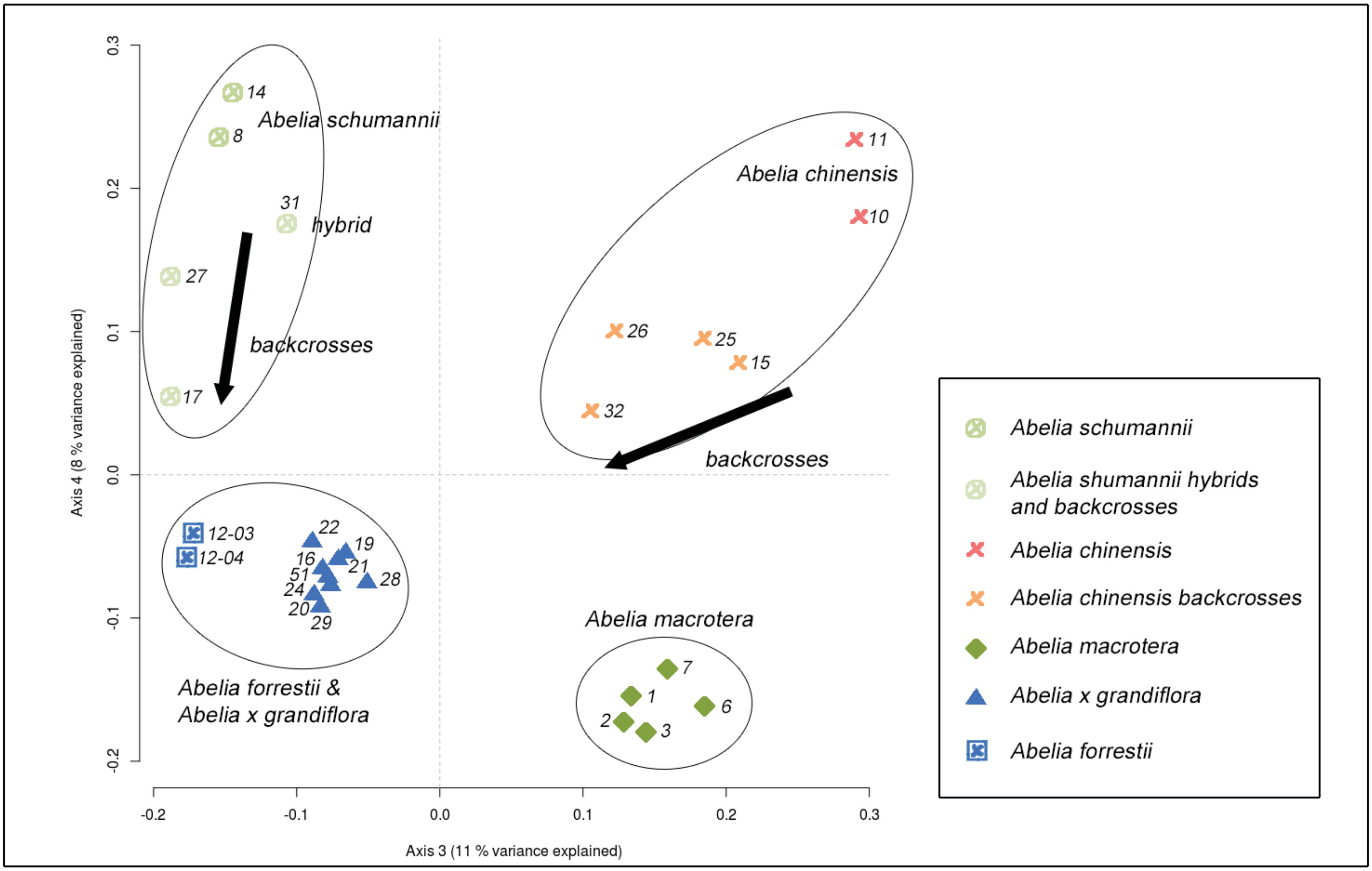


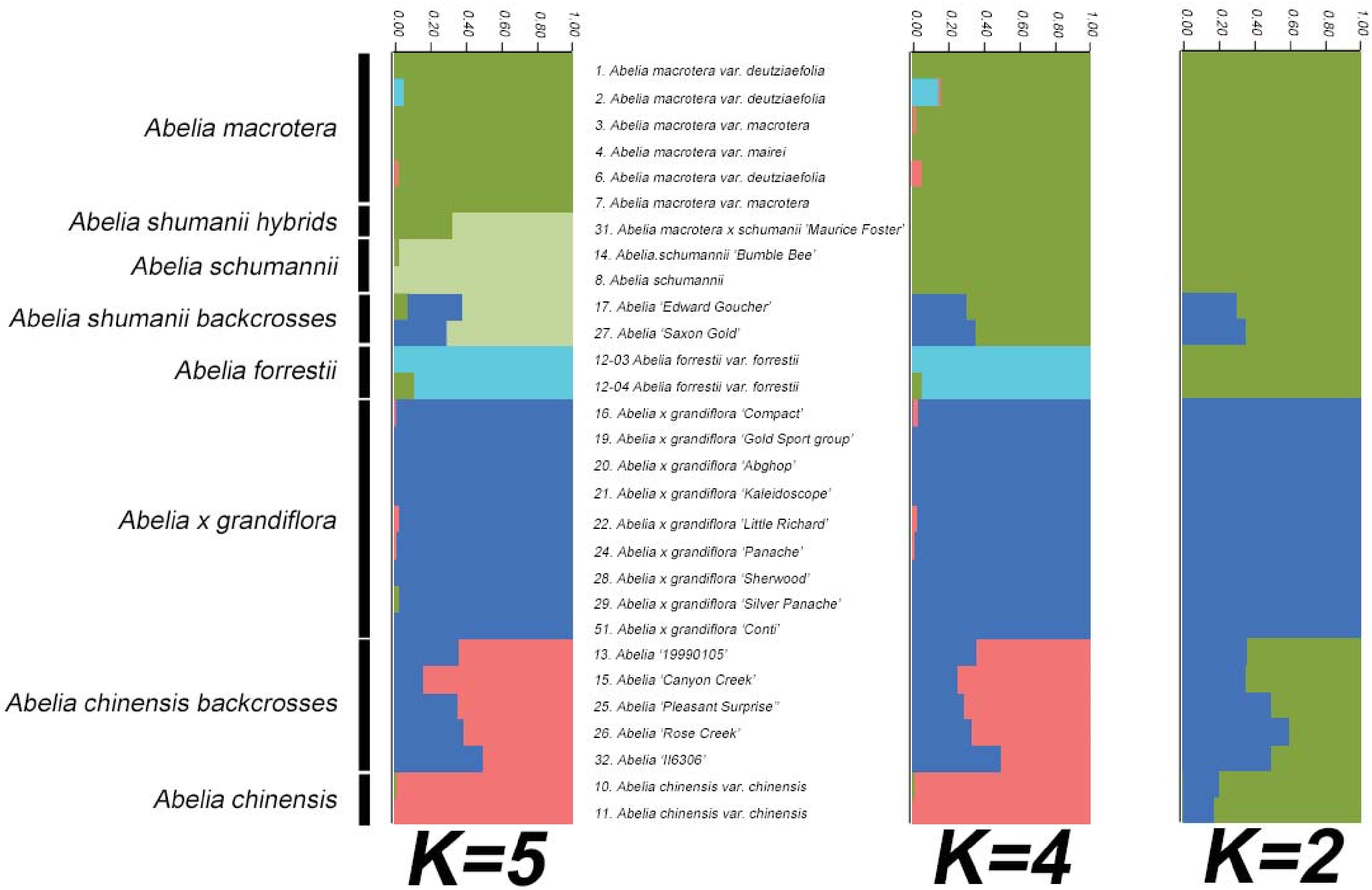
Abelia x grandiflora 'Francis Mason' 33
79/0.99
Abelia x grandiflora 34
78/1
Abelia x grandiflora 35
Abelia x grandiflora 36
Abelia chinensis var. chinensis 11
54/0.96
-/1
Abelia chinensis var. chinensis 37
63/0.98
Abelia chinensis var. chinensis 38
Abelia macrotera var. deutziaefolia 6
Abelia forrestii var. forrestii 12
99/1
Abelia forrestii var. gracilenta 39
Abelia macrotera var. mairei 40
Abelia macrotera var. macrotera 41
88/1
Abelia macrotera var. macrotera 42
96/1
Abelia schumannii 43
65/0.97
Abelia schumannii 8
Abelia macrotera var. engleriana 44
Abelia macrotera var. engleriana 45
77/0.99
Abelia macrotera var. macrotera 7
Abelia uniflora 46
Diabelia serrata 47
91/1
Dipelta yunnanensis 48
100/1
60/0.97
Kolkwitzia amabilis 49
Linnaea borealis var. borealis 50
Vesalea floribunda 52
Abelia x grandiflora
Abelia x grandiflora
(Zhejiang)
Abelia chinensis
Abelia macrotera backcross
Abelia forrestii
Abelia macrotera
Abelia schumannii
Abelia macrotera
Abelia uniflora
Outgroups



-/0.50
Dipelta yunnanensis 48
Kolkwitzia amabilis 49
Linnaea borealis var. borealis 50
84/1
Vesalea floribunda 52
Diabelia serrata 47
77/0.97
Abelia forrestii var. forrestii 12
99/1
Abelia forrestii var. gracilenta 39
Abelia chinensis var. chinensis 38
76/1
Abelia chinensis var. chinensis 37
-/0.57
Abelia x grandiflora 36
91/1
Abelia x grandiflora 34
Abelia uniflora 46
Abelia schumannii 43
Abelia macrotera var. mairei 40
78/1
Abelia macrotera var. engleriana 44
64/0.99
Abelia macrotera var. engleriana 45
Abelia macrotera var. macrotera 41
-/1
Abelia macrotera var. macrotera 42
Outgroups
Abelia forrestii
Abelia chinensis
Abelia x grandiflora
Abelia uniflora
Abelia schumannii
Abelia macrotera

29. Abelia x grandiflora 'Panache'
28. Abelia x grandiflora 'Sherwood'
51. Abelia x grandiflora 'Conti'
19. Abelia x grandiflora 'Gold Sport' group
20. Abelia x grandiflora 'Abghop'
16. Abelia x grandiflora 'Compact'
21. Abelia x grandiflora 'Kaleidoscope'
24. Abelia x grandiflora 'Panache'
22. Abelia x grandiflora 'Little Richard'
26. Abelia 'Rose Creek'
15. Abelia 'Canyon Creek'
32. Abelia 'II6306'
13. Abelia '19990105'
10. Abelia chinensis var. chinensis
11. Abelia chinensis var. chinensis
25. Abelia 'Pleasant surprise'
6 Abelia macrotera var. deutziaefolia (Guizhou, Guiyang)
4 Abelia macrotera var. mairei
7. Abelia macrotera var. macrotera (Sichuan)
3. Abelia macrotera var. macrotera (Hubei)
1. Abelia macrotera var. deutziaefolia (N. Guizhou)
2 Abelia macrotera var. deutziaefolia (Guizhou, Guiyang)
14. Abelia schumannii 'Bumble Bee'
8. Abelia schumannii
31. Abelia macrotera x schumanii 'Maurice Foster'
27. Abelia 'Saxon Gold'
17. Abelia 'Edward Goucher'
12-04 Abelia forrestii var. forrestii
12-03 Abelia forrestii var. forrestii
Abelia x grandiflora 'Sherwood'
Abelia x grandiflora 'Francis Mason'
Abelia x grandiflora 'Little Richard'
Abelia chinensis backcrosses
Abelia shumanii hybrids
and backcrosses
Abelia x grandiflora
Abelia chinensis
Abelia macrotera
Abelia schumannii
Abelia forrestii


Abelia schumannii
hybrid
backcrosses
Abelia chinensis
backcrosses
Abelia forrestii &
Abelia x grandiflora
Abelia macrotera
14
8
31
27
17
11
10
26
25
15
32
12-03
12-04
22
19
16
21
51
28
24
20
29
7
1
6
2
3
Axis 4 (8 % variance explained)
Axis 3 (11 % variance explained)
0.3
0.2
0.1
0.0
-0.1
-0.2
-0.2
-0.1
0.0
0.1
0.2
0.3
Abelia schumannii
Abelia shumannii hybrids and backcrosses
Abelia chinensis
Abelia chinensis backcrosses
Abelia macrotera
Abelia x grandiflora
Abelia forrestii



0.00
0.20
0.40
0.60
0.80
1.00
Abelia macrotera
Abelia shumanii hybrids
Abelia schumannii
Abelia shumanii backcrosses
Abelia forrestii
Abelia x grandiflora
Abelia chinensis backcrosses
Abelia chinensis
1. Abelia macrotera var. deutziaefolia
2. Abelia macrotera var. deutziaefolia
3. Abelia macrotera var. macrotera
4. Abelia macrotera var. mairei
6. Abelia macrotera var. deutziaefolia
7. Abelia macrotera var. macrotera
31. Abelia macrotera x schumanii 'Maurice Foster'
14. Abelia.schumannii 'Bumble Bee'
8. Abelia schumannii
17. Abelia 'Edward Goucher'
27. Abelia 'Saxon Gold'
12-03 Abelia forrestii var. forrestii
12-04 Abelia forrestii var. forrestii
16. Abelia x grandiflora 'Compact'
19. Abelia x grandiflora 'Gold Sport group'
20. Abelia x grandiflora 'Abghop'
21. Abelia x grandiflora 'Kaleidoscope'
22. Abelia x grandiflora 'Little Richard'
24. Abelia x grandiflora 'Panache'
28. Abelia x grandiflora 'Sherwood'
29. Abelia x grandiflora 'Silver Panache'
51. Abelia x grandiflora 'Conti'
13. Abelia '19990105'
15. Abelia 'Canyon Creek'
25. Abelia 'Pleasant Surprise"
26. Abelia 'Rose Creek'
32. Abelia 'II6306'
10. Abelia chinensis var. chinensis
11. Abelia chinensis var. chinensis
K=5
K=4
K=2

Abelia macrotera
var. deutziaefolia

Abelia uniflora

Abelia chinensis var. chinensis

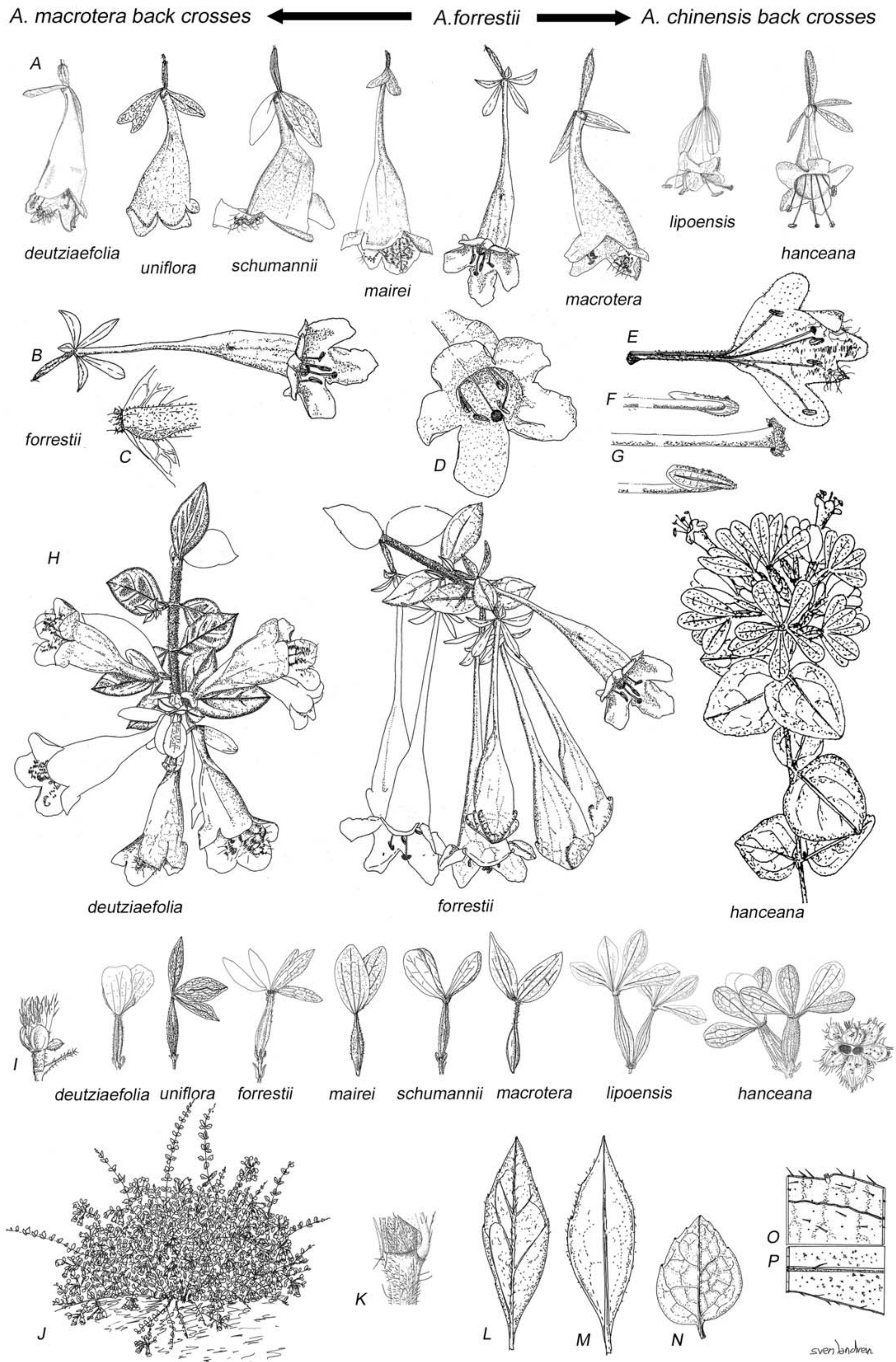
Abelia forrestii

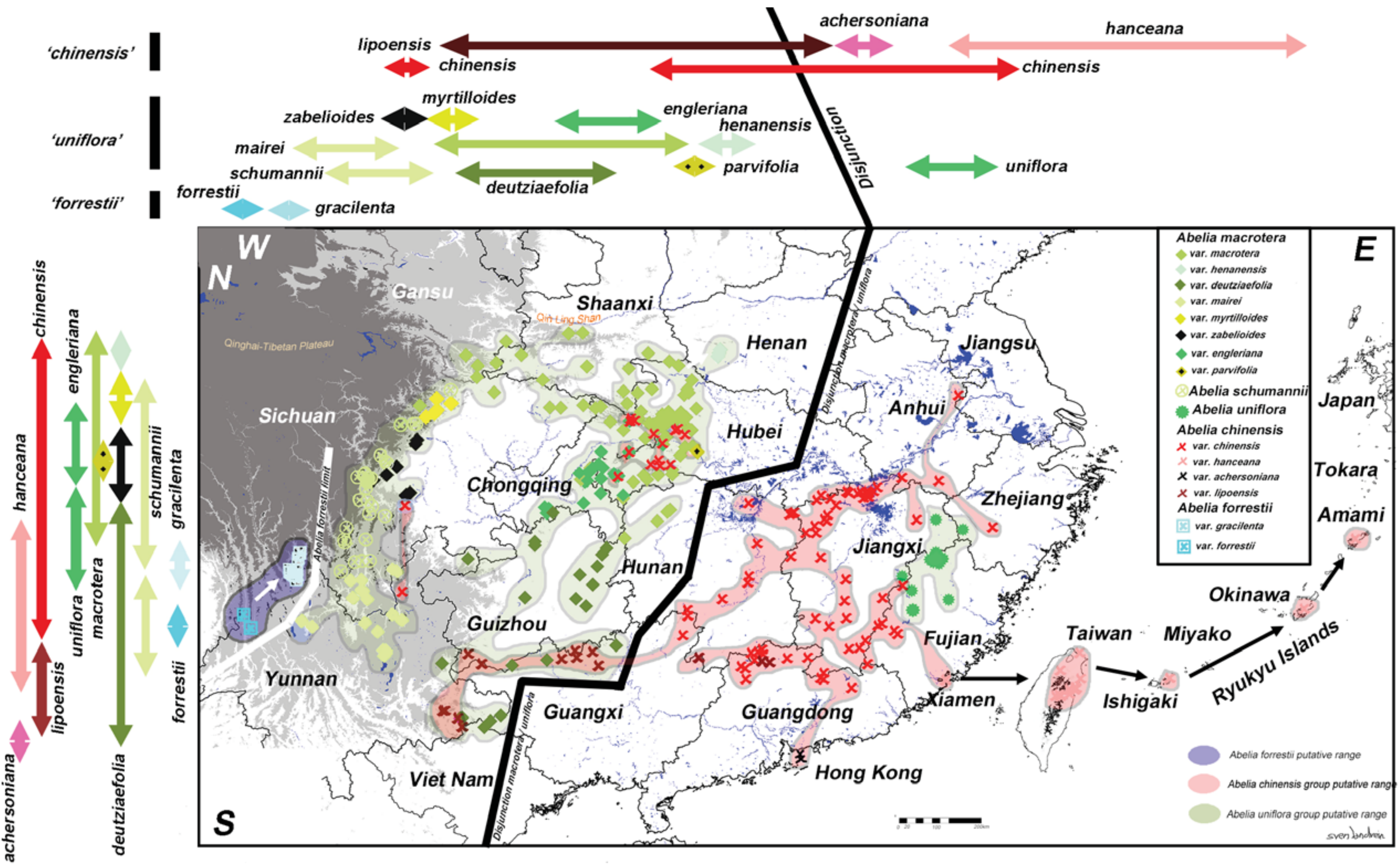
Abelia macrotera var. mairei

Abelia schumannii

Abelia 'Maurice Foster'

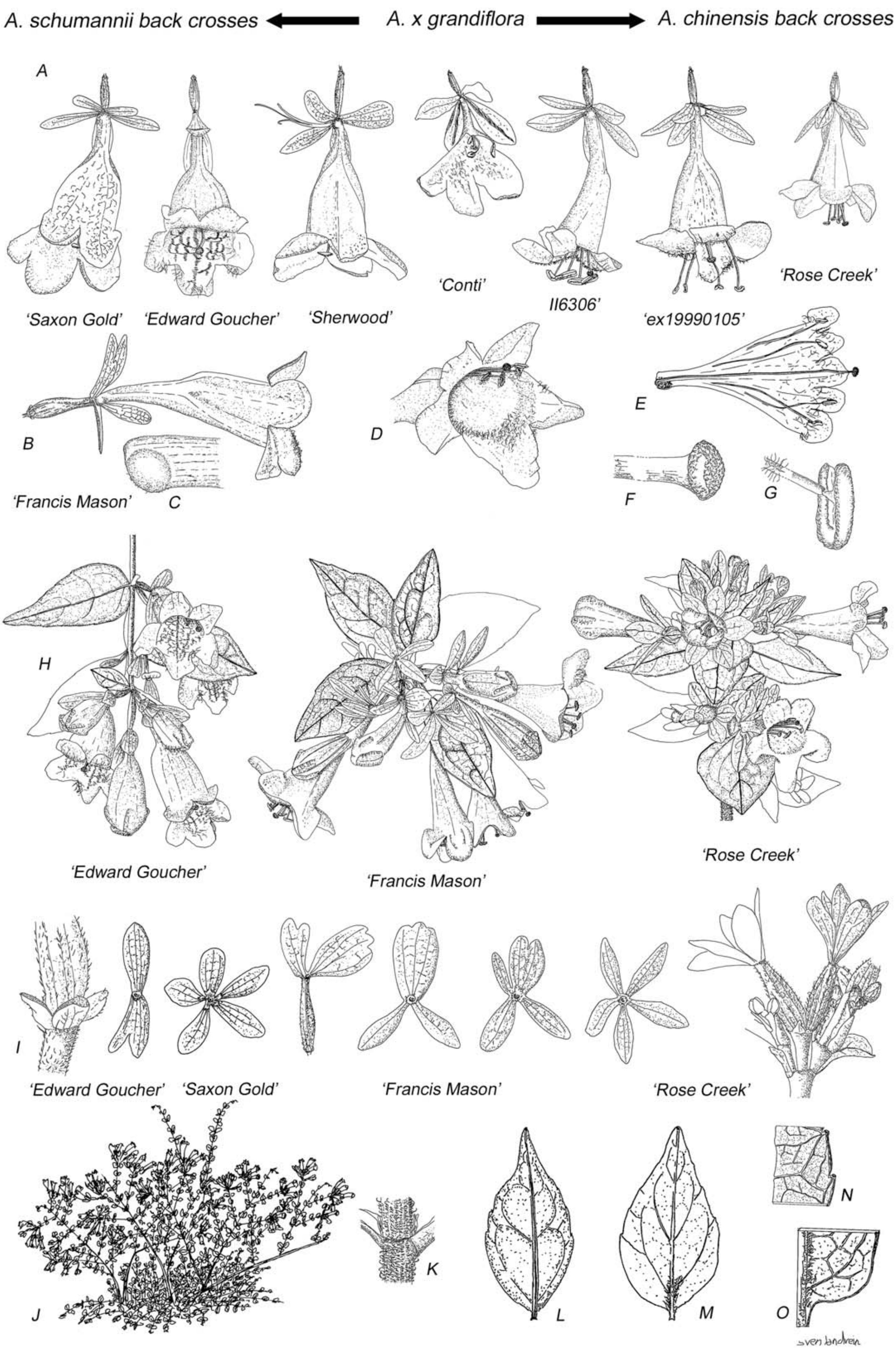
Abelia macrotera var. macrotera


A. macrotera back crosses
A.forrestii
A. chinensis back crosses
A
deutziaefolia
uniflora
schumannii
mairei
macrotera
lipoensis
hanceana
B
forrestii
C
D
E
F
G
H
deutziaefolia
forrestii
hanceana
I
deutziaefolia
uniflora
forrestii
mairei
schumannii
macrotera
lipoensis
hanceana
J
K
L
M
N
O
P
sven landrein



'chinensis'
lipoensis
chinensis
achersoniana
hanceana
chinensis
'uniflora'
zabelioides
myrtilloides
engleriana
henanensis
mairei
schumannii
deutziaefolia
parvifolia
uniflora
'forrestii'
forrestii
gracilenta
Disjunction
W
N
E
S
Gansu
Shaanxi
Qin Ling Shan
Qinghai-Tibetan Plateau
Sichuan
Henan
Jiangsu
Anhui
Hubei
Chongqing
Hunan
Zhejiang
Jiangxi
Guizhou
Yunnan
Guangxi
Guangdong
Fujian
Xiamen
Hong Kong
Viet Nam
Taiwan
Miyako
Ishigaki
Okinawa
Ryukyu Islands
Amami
Tokara
Japan
Abelia forrestii limit
Disjunction macrotera/ uniflora
Abelia macrotera
var. macrotera
var. henanensis
var. deutziaefolia
var. mairei
var. myrtilloides
var. zabelioides
var. engleriana
var. parvifolia
Abelia schumannii
Abelia uniflora
Abelia chinensis
var. chinensis
var. hanceana
var. achersoniana
var. lipoensis
Abelia forrestii
var. gracilenta
var. forrestii
Abelia forrestii putative range
Abelia chinensis group putative range
Abelia uniflora group putative range
chinensis
hanceana
engleriana
uniflora
macrotera
lipoensis
achersoniana
schumannii
gracilenta
forrestii
deutziaefolia

Abelia schumannii* backcrosses** ***Abelia x grandiflora ***Abelia chinensis* backcrosses**


A. schumannii back crosses
A. x grandiflora
A. chinensis back crosses
A
'Saxon Gold'
'Edward Goucher'
'Sherwood'
'Conti'
II6306'
'ex19990105'
'Rose Creek'
B
'Francis Mason'
C
D
E
F
G
H
'Edward Goucher'
'Francis Mason'
'Rose Creek'
I
'Edward Goucher'
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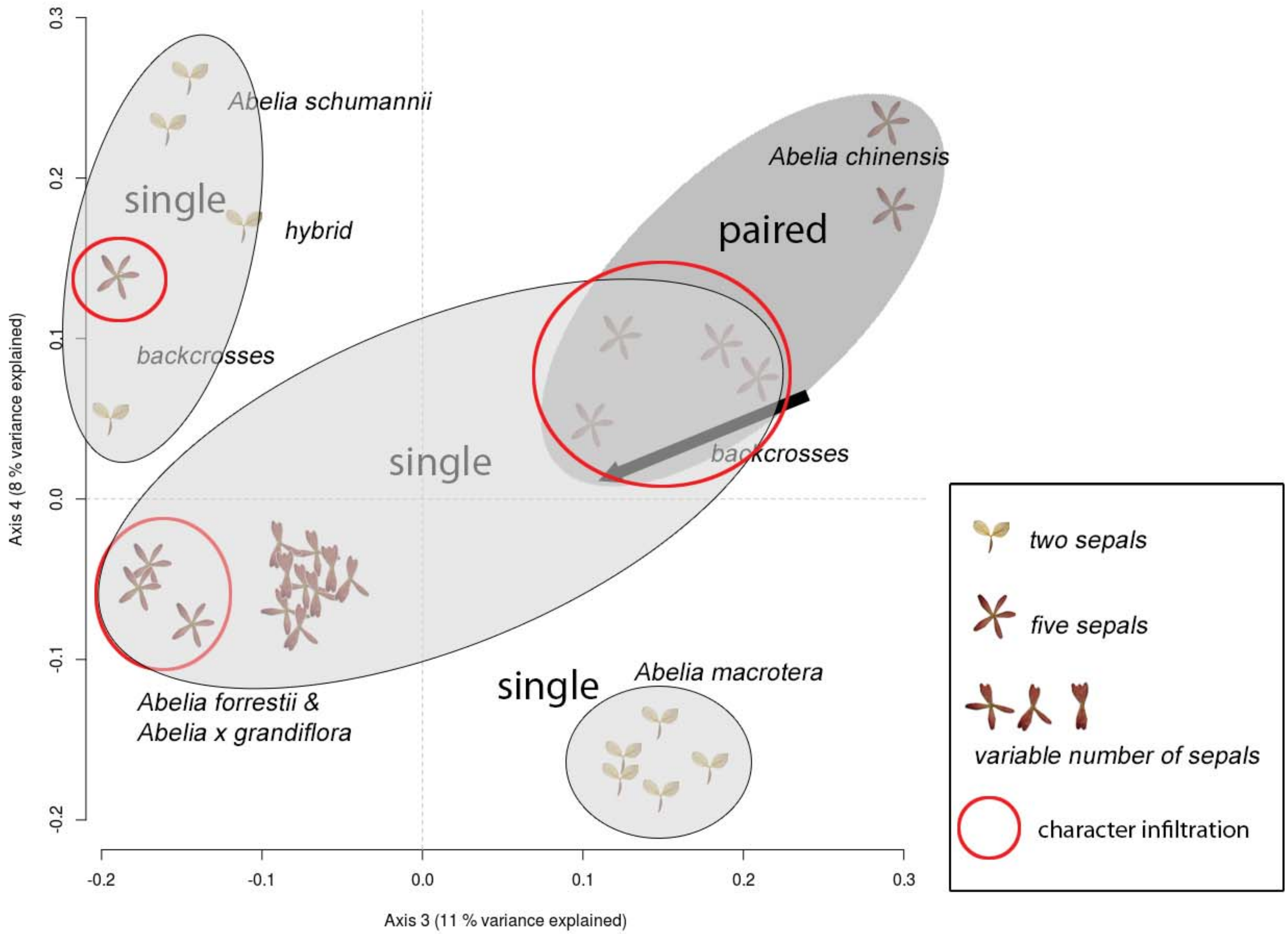
'Francis Mason'
'Rose Creek'
J
K
L
M
N
O



Abelia schumannii
single
hybrid
backcrosses
Abelia chinensis
paired
single
backcrosses
Abelia forrestii &
Abelia x grandiflora
single
Abelia macrotera
two sepals
five sepals
variable number of sepals
character infiltration
Axis 3 (11 % variance explained)
Axis 4 (8 % variance explained)